SOME ASPECTS OF EARTHWORM ECOLOGY

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The earthworm populations of a series of grass plots receiving various manurial treatments were compared in relation to physical, chemical and biotic factors of the soil. Soil pH *and exchangeable calcium were found to be highly correlated with earthworm numbers, and laboratory experiments confirmed the sensitivity of some species of earthworm to hydrogen ion concentration. It was concluded that extreme soil acidities were more important in limiting the distribution of earthworms than deficiencies in calcium supply. Thirty-six woodland sites in the Lake District were sampled and the earthworm species found there were classified as acid tolerant, ubiquitous or acid intolerant. Aggregated populations of some species of earthworms were found in some of the grass plots and in a neighbouring pasture field. Although some of the aggregation may have been due to variations in soil conditions there was evidence that the balance between the aggregating effects of reproduction and the randomizing effects of mortality and dispersal also affected the earthworm distribution pattern.*

In mull soils earthworms commonly dominate the soil fauna and constitute more than half the biomass. There are in Great Britain at least 26 indigenous species of which about 10 are common field species.

A comprehensive study by EVANS and GUILD (1947, 1948a) and GUILD (1948) of most of these field species showed the effects of arable and ley cultivation practices on field populations and the importance of soil type in earthworm distribution. Their work also included laboratory studies of the life cycles of some species and the effects of soil moisture, soil temperature and food supply on cocoon production.

However, the relative importance of these and other ecological factors in determining earthworm population densities required further exploration in the field and a convenient site was available where six of the common species could be studied under a wide range of soil conditions.

This site, known as Park Grass, is an experimental grass field of approximately seven acres at Rothamsted Experimental Station. In 1856 it was divided into plots, mostly of $\frac{1}{4}$ acre, which have since received regular manurial treatments including organic manures

and a variety of inorganic fertilizers (*Figure 36*). The plots are subdivided into limed and unlimed sections which have developed characteristic differences in soil conditions, fauna and herbage, and have now reached a fairly stable state of biological equilibrium with their manurial treatments.

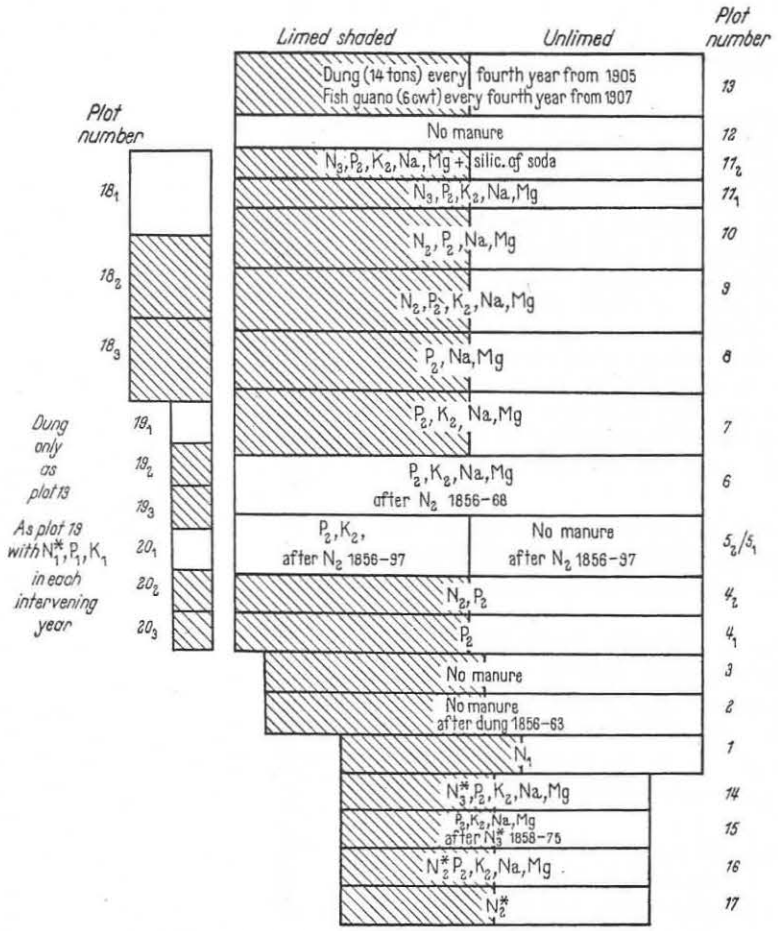

Figure 36—The Park Grass plots.

N_1 N_2 N_3	*2, 4, 6 cwt. Sulphate of ammonia per acre*
N_1^* N_2^* N_3^*	*1½, 2½, 5 cwt. Nitrate of soda*
P_1 P_2	*2, 3½ cwt. Superphosphate*
K_1 K_2	*1, 4½ cwt. Sulphate of potash*
Na	*1 cwt. Sulphate of soda*
Mg	*1 cwt. Sulphate of magnesia*

2,000 lb. ground lime per acre applied every fourth year (1948, 1952) to shaded halves of plots. Most plots are ½ acre, but the sizes range from ⅓ to 1⅓ acre.

An additional advantage of these plots for an ecological study was the existence of a fund of information from previous investigations of the site. This was supplemented to provide numerical data on soil moisture, organic matter, nitrogen content, calcium content and acidity, yield and composition of vegetation, arthropod populations, and the activity of moles.

A selection of plots, providing a range of these factors, was sampled for earthworms during mid-March to mid-April in 1951 and 1952. In view of the experimental character of the plots the standard potassium permanganate method of sampling was unsuitable and an electrical technique, described on pages 356–364, was developed. Population estimates were obtained for 18 plots in 1951 and 11 plots in 1952 and the habitat data and population estimates were examined for numerical relationship. Eight species were collected and of these six were sufficiently numerous for regression analysis. These were *Allolobophora caliginosa* (Sav.), *A. nocturna* Ev., *Eisenia rosea* (Sav.), *Lumbricus castaneus* (Sav.), *L. terrestris* L., and *Octolasium cyaneum* (Sav.).

Small numbers of *Allolobophora chlorotica* (Sav.) and *Lumbricus rubellus* Hoffm. were also taken. The 'forma' *macedonica* (Rosa) of *Eisenia rosea* was present with the typical form but, on account of the difficulty of separating immature specimens, the two forms were classed together.

SOIL

Moisture

No relationship was detected between the earthworm populations and the percentage moisture content of the soils from different plots. The data of Table 20, based on monthly determinations made by H. L. Richardson (unpublished) in 1931–33, show that the differences between plots in moisture content were very small, especially by comparison with seasonal differences within plots. An additional set of determinations was made in May 1952 and agreed closely with the comparable values obtained by Richardson.

Organic matter

A. C. Evans (unpublished) found at Rothamsted that the Broadbalk plots treated with organic manure had higher populations than control plots and, on Park Grass, this was also the case for *A. caliginosa*, *A. nocturna*, *L. castaneus* and *O. cyaneum*. The effect of organic manuring was, however, masked in the analysis by the presence of accumulated plant debris on the plots with low earthworm populations and the regressions on organic carbon, nitrogen

TABLE 19. Earthworm populations of Park Grass plots (numbers of earthworms per one square foot)

Plot		Treatment	*A. caliginosa* 1951	*A. caliginosa* 1952	*A. nocturna* 1951	*A. nocturna* 1952	*E. rosea* 1951	*E. rosea* 1952	*L. castaneus* 1951	*L. castaneus* 1952
1	U	N1	0	—	0	—	0·18±0·36	—	0	—
	L		1·06±0·43	—	0·27±0·33	—	3·19±1·59	—	2·40±0·89	—
3	U	Control	0·65±0·29	0·27±0·60	0·39±0·36	0·12±0·26	7·06±2·11	0·93±1·18	3·30±2·32	1·49±0·60
	L		1·29±1·03	1·45±1·13	0·07±0·14	0·16±0·33	5·24±2·51	1·27±1·21	4·31±2·10	1·08±0·58
4_2	U	N4, P3½	0	0	0	0	0	0	0	0·07±0·23
	L		0·70±0·32	—	0	—	0·75±0·62	—	1·01±0·43	—
7	U	P3½, K4½, Na1, Mg1	0·60±0·80	0·24±0·47	1·42±1·35	0·74±0·51	1·05±0·93	0·16±0·50	1·72±0·75	0·44±0·57
	L		3·08±1·71	1·84±1·01	0·18±0·36	0·11±0·39	14·00±4·93	5·43±4·03	4·80±1·49	1·47±1·08
8	U	P2½, Na1, Mg1	0·60±0·42	—	0·38±0·30	—	1·13±0·44	—	1·21±0·73	—
	L		2·35±0·31	—	0·09±0·17	—	5·31±2·44	—	3·79±3·23	—
9	U	N4, P3½, K4½, Na1, Mg1	—	0	—	0	—	0	—	0
	L		—	1·22±1·16	—	0	—	1·17±1·52	—	0·64±1·01
11_1	U	N6, P3½, K4½, Na1, Mg1	0	—	0	—	0	—	0·09±0·17	—
	L		0·10±0·10	—	0	—	0	—	0·12±0·23	—
13	U	Dung	0·21±0·25	0·74±0·29	1·84±0·76	1·76±0·65	1·51±0·95	1·98±1·98	3·21±0·71	5·54±3·49
	L		6·12±1·17	5·13±2·61	1·16±0·71	0·75±0·44	5·35±2·52	3·96±2·06	7·05±4·01	3·63±1·62
14	U	N*5, P3½, K4½, Na1, Mg1	2·68±1·30	5·75±2·91	0·18±0·36	0·34±0·33	2·32±1·10	1·73±1·11	0·97±0·53	1·58±0·70
	L		—	2·42±1·47	—	0·09±0·18	—	3·10±1·55	—	1·57±0·77
17	L	N*2½	0·61±0·61	—	0·77±0·23	—	2·20±0·60	—	1·49±0·13	—
19_1	U	Dung	1·59±0·78	—	0·78±0·32	—	1·94±0·67	—	3·65±2·54	—
20_3	L	Dung +N*1½, P2, K1	2·34±0·72	—	1·24±0·78	—	2·95±1·66	—	2·76±0·91	—

Plot		Treatment	*L. terrestris* 1951	*L. terrestris* 1952	*O. cyaneum* 1951	*O. cyaneum* 1952	Total (all species) 1951	Total (all species) 1952
1	U	N1	0·10±0·18	—	0·10±0·20	—	0·38±0·75	—
	L		2·42±1·45	—	0·82±0·57	—	12·71±5·14	—
3	U	Control	1·84±0·43	1·22±0·42	2·43±0·92	0·64±0·62	16·59±2·25	4·82±1·85
	L		2·14±0·99	2·53±0·82	0·98±0·61	0·49±0·48	15·42±6·03	7·61±3·27
4_2	U	N4, P3½	0	0·03±0·11	0·26±0·51	0·07±0·23	0·26±0·51	0·18±0·46
	L		1·39±0·63	—	1·32±0·25	—	5·16±1·25	—
7	U	P3½, K4½, Na1, Mg1	1·56±0·59	1·18±0·53	2·22±0·59	1·73±1·11	8·88±4·89	4·49±2·19
	L		3·37±0·47	2·02±0·92	1·11±0·51	0·62±0·41	27·82±5·33	11·42±5·12
8	U	P2½, Na1, Mg1	0·61±0·46	—	1·67±0·67	—	5·78±2·16	—
	L		1·55±0·18	—	0·88±0·36	—	15·25±6·54	—
9	U	N4, P3½, K4½, Na1, Mg1	—	0	—	0·05±0·15	—	0·05±0·15
	L		—	1·07±0·85	—	0·90±0·48	—	4·00±3·54
11_1	U	N6, P3½, K4½, Na1, Mg1	0	—	0	—	0·09±0·17	—
	L		0·10±0·18	—	0·17±0·34	—	0·48±0·96	—
13	U	Dung	1·95±1·45	2·09±0·73	2·73±1·59	2·28±1·20	11·64±3·91	12·08±5·79
	L		2·68±1·22	2·38±0·59	1·00±0·52	0·60±0·54	24·49±5·00	14·25±3·76
14	U	N*5, P3½, K4½, Na1, Mg1	1·33±0·24	1·50±0·86	0·58±0·26	0·32±0·25	8·19±1·84	9·77±4·75
	L		—	1·30±0·77	—	0·27±0·42	—	7·44±2·49
17	L	N*2½	1·56±0·26	—	0·57±0·37	—	7·18±1·06	—
19_1	U	Dung	1·10±0·40	—	1·24±0·35	—	10·52±2·62	—
20_3	L	Dung +N*1½, P2, K1	2·11±0·62	—	0·93±0·47	—	13·16±0·85	—

Plot		*A. chlorotica* 1951
1	L	0·64±0·61
3	L	0·69±0·48
		1952
3	U	0·15±0·34
3	L	0·53±0·88
		L. rubellus
		1952
3	L	0·10±0·69

1951—Means of 4 samples 1952—Means of 10 samples

L = limed U = unlimed

N* Nitrate of soda N Sulphate of ammonia Na Sulphate of soda Mg Sulphate of magnesia K Sulphate of potash P Superphosphate

Figure following symbol = cwts. per acre

TABLE 20

Soil analyses, vegetation and fauna of some Park Grass plots
(all analyses refer to air-dry soil)

Plot	Soil moisture 1931–33 Mean %	Max. %	Min. %	Loss on ignition %	Organic carbon %	Nitrogen %	pH	Exchangeable calcium m. eq. per 100g	% Herbage 1947 Leguminosae	Agrostis vulgaris	Anthoxanthum odoratum	Arrhenatherum avenaceum	Dactylis glomerata	Holcus lanatus	Mole-hills per plot 1951	1952	Chiloplola Means of 5 2-inch cores	Staphylinidae Means of 5 2-inch cores
1 U	—	—	—	—	—	—	4·6	2·75	0	76·0	0·3	0·2	2·0	0	0	0	2·4	1·2
L	—	—	—	—	—	—	6·8	14·45	3·7	1·1	6·0	4·2	15·9	5·9	0	0	2·4	1·6
3 U	27·6	32·3	10·0	9·94	3·60	0·288	5·3	9·25	11·0	8·4	5·1	0·6	12·1	5·3	43	30	3·2	0·2
L	27·4	32·3	9·7	10·71	3·76	0·314	7·0	16·75	15·2	1·1	2·6	0·1	3·5	5·0	0	0	2·8	0·2
4_2 U	—	—	—	12·03	—	—	4·1	0·67	0	68·8	14·5	0	0	4·8	0	0	0·6	0·8
L	—	—	—	—	—	—	5·6	13·63	0·1	1·8	4·6	2·3	0·1	1·0	0	0	3·0	1·2
7 U	23·5	27·7	9·4	8·20	2·70	0·235	5·0	5·10	17·7	4·7	6·7	4·0	20·8	1·8	0	0	4·8	0·6
L	24·9	29·7	9·3	9·70	3·06	0·266	6·8	13·95	9·1	0·1	0·3	19·2	20·7	0·6	155	200	1·6	0
8 U	—	—	—	—	—	—	5·1	9·35	9·8	4·2	5·8	12·4	10·9	6·5	0	0	1·6	1·2
L	—	—	—	—	—	—	6·8	18·15	10·3	0·9	5·6	8·3	6·2	4·2	100	20	0·8	0·2
9 U	26·9	33·5	13·8	11·67	3·91	0·302	4·1	0·63	0	23·8	15·7	4·3	0·2	51·3	0	0	—	—
L	27·1	32·5	10·4	12·04	3·87	0·309	5·1	11·15	6·0	3·4	12·4	13·2	12·5	3·4	0	0	—	—
11_1 U	—	—	—	—	—	—	4·0	1·41	0·2	4·5	0·8	0·3	0	81·1	0	0	0·2	1·4
L	—	—	—	—	—	—	4·4	5·20	0	0·8	0·7	2·9	2·5	7·6	0	0	0·6	0
13 U	26·3	30·5	10·8	8·82	2·97	0·250	4·6	4·70	0·7	10·9	14·2	2·1	9·8	6·2	135	10	2·2	0·4
L	27·7	31·9	11·0	9·82	3·45	0·280	6·4	15·00	7·5	0·2	0·8	14·2	24·2	5·3	530	500	2·6	0
14 U	26·8	31·3	9·7	9·71	3·10	0·265	5·9	9·60	3·3	0·5	0·2	36·8	14·5	0·8	225	115	1·4	1·0
L	26·9	31·0	9·4	9·49	3·58	0·297	6·9	15·25	12·9	0·6	0·4	35·4	8·0	0·2	0	0	3·0	1·0
17 L	—	—	—	—	—	—	7·0	15·85	2·7	—	—	—	—	—	88	130	1·8	0·4
19_1 U	—	—	—	—	—	—	5·8	10·20	17·0	—	—	—	—	—	160	45	—	—
20_2 L	—	—	—	—	—	—	6·6	11·65	10·3	—	—	—	—	—	160	50	—	—

L=limed U=unlimed

content and loss on ignition were negative. The carbon and nitrogen values (from RICHARDSON, 1938) are in general closely related, with only small fluctuations around a mean C/N ratio of 12·1, and Richardson concluded from this that the nitrogen content was a fair index to the total organic matter content of the soils. This measure, as with loss on ignition, while it fails to distinguish soil organic matter in the terms most relevant to earthworm nutrition, indicates that other factors affecting the earthworm distribution were of over-riding importance.

Acidity

The pH values, which are taken from the Rothamsted farm guide (Rothamsted Experimental Station, 1947), showed a significant positive relationship with *A. caliginosa*, *E. rosea* and *L. terrestris* in 1951 and 1952, and with *L. castaneus* in 1951.

Calcium content

Determinations of the exchangeable calcium of the Park Grass plots were made by Dr. H. H. Le Riche of the Rothamsted Pedology Department in 1952. The values, expressed as milli-equivalents per 100 grammes, agreed very closely for pairs of samples, comprising eight auger borings to a depth of nine inches, which were determined for each plot. The regressions of earthworm populations on exchangeable calcium were significant at the 5 per cent probability level for *A. caliginosa*, *E. rosea* and *L. terrestris* in 1951 and 1952, and for *L. castaneus* in 1951 and at the 10 per cent level in 1952.

VEGETATION

The vegetation of Park Grass has been analysed for many years by the Botany Department at Rothamsted, and of the many plant species recorded those which comprised more than 15 per cent of the herbage in 1939, 1940, 1947 and 1948, when the analyses were most complete, were considered in relation to the earthworm populations. The figures for 1947, when most of the plots were recorded, were used for regression analysis and significant regressions were obtained for *Arrhenatherum avenaceum*, *Agrostis vulgaris*, *Anthoxanthum odoratum*, *Dactylis glomerata* and *Holcus lanatus*. The regressions on *Alopecurus pratensis*, *Avena pubescens*, *Festuca ovina* and the total weights of herbage were not significant.

Leguminosae

BATES (1933) observed a relation between the incidence of worm-casts and *Trifolium repens* and thought that close mowing or grazing

favoured clover by reducing competition from other plants for light and also increased the number of earthworms by reducing the loss of soil moisture by plant transpiration. HOPP and SLATER (1948) grew clover in barrels and attributed high yields to an improvement of soil structure by earthworm activity. On the Park Grass plots, regressions on the percentage of Leguminosae in the herbage sampled in 1947 were significant and positive at the 5 per cent level of probability for the 1951 populations of *E. rosea*, *L. terrestris* and *L. castaneus* and for *A. caliginosa* at the 10 per cent level.

FAUNA

A census of the arthropod populations of the Park Grass plots made by Raw (*in litt.*), 1950, included population estimates of the Chilopoda and Staphylinidae which are known to include species predacious on earthworms. The regressions were negative and significant at the 5 per cent level for *E. rosea* on Chilopoda in 1952 but not in 1951, and for *L. castaneus* on Staphylinidae in 1951 but not in 1952. The results were therefore regarded as inconclusive.

Moles, which are also known as earthworm predators, were present on some of the plots and the numbers of mole-hills were counted in March of 1951 and 1952. Of six regressions which were significant up to the 10 per cent level, five were positive and indicated that the moles tended to occur where the earthworm populations were highest, but were not responsible for their scarcity on the plots with low populations.

FACTORS INFLUENCING DISTRIBUTION OF EARTHWORMS ON 'PARK GRASS'

To summarize the investigation so far, of the 264 regression values calculated, 44 were significant at the 5 per cent probability level and the occurrence of five grasses and Leguminosae, the soil pH and exchangeable calcium, were found to be numerically related to the earthworm populations. It remains to separate those factors which do not really influence the earthworm distribution but are related only by associated factors and this can be achieved in part by multiple regression analysis.

The partial regressions for the five grasses and Leguminosae were calculated, taking pH as an additional variate. For *Agrostis*, *Anthoxanthum*, *Holcus* and Leguminosae these were not significant and the relationship of these plants to the earthworm populations can therefore be regarded as indirect. The partial regression of *Arrhenatherum* and *Dactylis* were significant for the 1951 earthworm population figures but not for those of 1952 and the effect, if any,

of these two grasses on earthworm distribution remains unsubstantiated. Of the factors examined so far, there remain only pH and exchangeable calcium which seem likely to have a substantial effect on the distribution of earthworms.

RELATIONSHIP OF SOIL ACIDITY AND EXCHANGEABLE CALCIUM TO EARTHWORM POPULATIONS

It is generally agreed that earthworms are scarce in very acid soils, but is this the result of a nervous sensitivity to soil acidity or of nutritional requirements which acid soils fail to meet ?

WIELER (1914) notes that mor (Torf) soils in which he found no earthworms were lacking in calcium salts which he thought necessary to the worms in order to replace loss by the calciferous glands.

NIELSON (1951) found that field populations of *A. caliginosa* in New Zealand were more highly correlated with exchangeable calcium in the soil than with its pH, and concluded that shortage of calcium was the more important factor affecting earthworm distribution. These observations support the view expressed by RUSSELL (1950) that ' most earthworms, including all the larger species, need a continuous supply of calcium which they convert into calcium carbonate and excrete from special glands in their digestive tract. Earthworms are therefore absent on very acid soils or soils devoid of calcium.'

However, the fact that on a calcium-rich diet earthworms excrete calcium is not of itself adequate evidence for concluding that calcium deficiency is the operative factor limiting earthworm populations in acid soils.

On the Park Grass plots, the population estimates of *A. caliginosa*, *E. rosea* and *L. terrestris* for both years, and *L. castaneus* in one year, were significantly related to both pH and exchangeable calcium. These two factors were too highly correlated for multiple regression analysis but, by calculating the variance accounted for by each, it was shown that for six of the seven populations more of the differences between plots could be explained by pH than by calcium content (Table 21).

However the difference between the percentages of the variance explained was small, the average for the seven regressions on pH being 54 per cent compared with 52 per cent for exchangeable calcium, and supplementary evidence was sought from laboratory observations.

HURWITZ (1910) and others used the method of PARKER and METCALF (1906) to demonstrate the sensitivity of *Eisenia foetida* to hydrogen ion concentration, and a similar procedure was used for the species encountered on Park Grass.

TABLE 21

Percentage of ' between plots ' variance explained by regression of exchangeable calcium and pH on earthworm populations

1951 (18 plots)	*Regressions*		*% Variance explained*	
	pH	*Calcium*	pH	*Calcium*
A. caliginosa	0·556±0·123	0·103±0·025	53·16	48·39
E. rosea	0·774±0·158	0·144±0·032	57·63	53·75
L. castaneus	0·577±0·138	0·110±0·027	49·00	47·87
L. terrestris	0·490±0·091	0·087±0·020	61·83	52·86
1952 (11 plots)				
A. caliginosa	0·551±0·173	0·103±0·033	47·67	46·50
E. rosea	0·549±0·042	0·103±0·025	62·06	60·93
L. terrestris	0·357±0·112	0·071±0·020	47·91	54·00

Freshly dug worms were suspended by suction from a tube so that the anterior 6–7 segments were submerged in a beaker of distilled water. After a few seconds of initial wriggling the worm under test extended into the water and the number of seconds in which it remained submerged during the next minute was recorded. The beaker of water was then replaced by a dilute solution of sulphuric acid and the time of immersion was recorded for the next minute. By repeating this process the immersion time for each worm was recorded in successive minutes in solutions of pH 5·2 (distilled water), 3·2, 3·0, 2·8, 2·6, 2·4 and 2·2 and this was followed immediately by a repetition of the same run.

Five specimens each of *A. caliginosa*, *A. nocturna*, *E. rosea* and *L. terrestris* were tested. The reaction time for all species (*Figure 37*) was substantially the same and showed a striking contrast between the quiescent behaviour in solutions at pH 5·8, 3·2 and 3·0, and the violent contraction away from those of pH 2·6, 2·4 and 2·2. At pH 2·8 the reaction was intermediate and more variable but, despite the highly unnatural conditions of the experiment, the worms were capable of distinguishing between solutions differing in pH by less than half a unit.

Although this provided evidence, in support of earlier workers, of the sensitivity of earthworms to hydrogen ion concentration, this was only detected, perhaps because of the artificial conditions of the experiment, in solutions much more acid than any of the soils on Park Grass.

Another experiment was therefore carried out to observe the reactions of earthworms to the Park Grass soils direct. Soil was taken from nine of the plots, air-dried, sieved and moistened to

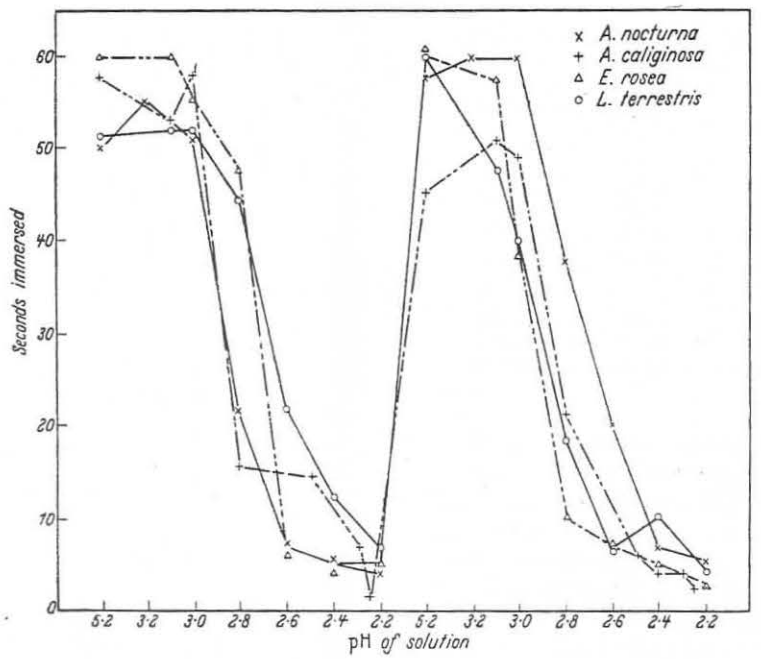

Figure 37—Relation between time during which earthworms remained immersed in acid solutions and the pH *of the solutions.*

30 per cent moisture content with distilled water. Five subsamples from each were put into glass jars which were numbered and arranged in a group at random. Four mature specimens of *A. chlorotica*, a species of convenient size, were placed on the soil surface of each jar and the time taken for the worms to bury themselves was recorded (*Figure 38*).

The pH values of the soils were 4·0, 4·1, 4·4, 5·0, 5·1, 5·6, 5·8, 6·9 and 7·0, and with those above pH 5·0 there was no significant difference between the times taken by the worms to burrow beneath the surface. Of the 120 worms in these six soils 96 had buried themselves after 1½ hours and after 21 hours only four remained partly exposed at the surface. In the three most acid soils the worms at first showed a violent avoidance reaction. After a short initial period in which they twisted themselves into knots, jerking convulsively and exuding coelomic fluid from the dorsal pores, they extended to their full length and crawled rapidly about the soil surface, intermittently raising and waving the anterior segments.

The activity them became sporadic and after one to two hours of intermittent wandering they remained motionless and extended with the body wall gradually losing tone. Two worms crawled into crevices between the soil and the glass of the containers but after 21 hours all the remaining 58 worms lay dead on the surface.

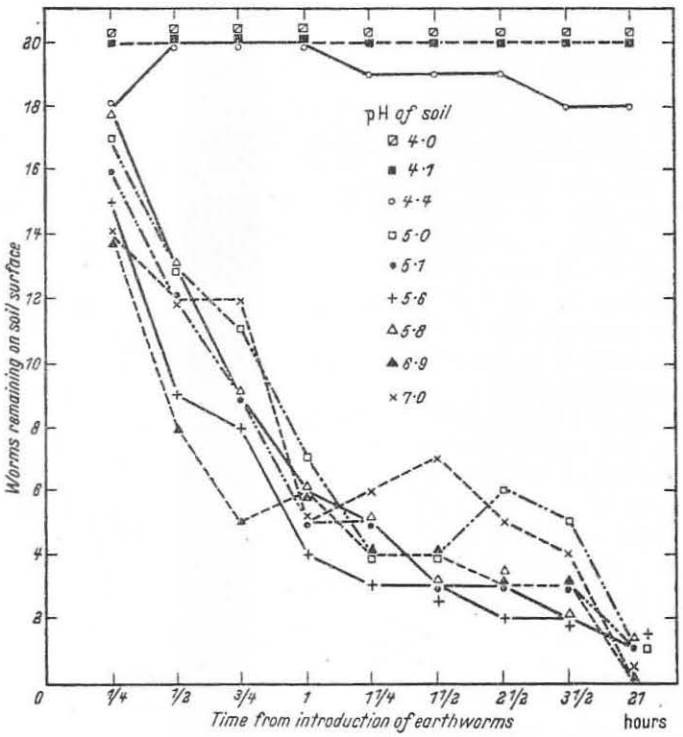

Figure 38—Relation between time taken by A. chlorotica *to burrow into soil, and the soil's acidity.*

In view of these observations it seems likely that earthworms would be repelled from the very acid field plots and that there would be little occasion for calcium deficiency, as a nutritional factor, to become operative. Taking this in conjunction with the high correlation between pH and the earthworm populations, and the demonstrable sensitivity to pH of 4 of the species concerned, we may infer that hydrogen ion concentration provides an explanation of the scarcity of earthworms on the most acid plots of Park Grass.

Since the acid soils of Park Grass owe their low pH values to repeated heavy applications of sulphate of ammonia, it remains to

confirm the relationship of pH and earthworm populations under natural field conditions.

RELATIONSHIP OF EARTHWORM DISTRIBUTION AND SOIL pH IN SOME LAKE DISTRICT WOODLANDS

The effect of hydrogen ion concentration on earthworms was studied by ARRHENIUS (1921), who recorded the survival times of worms placed in plots of soil which had been adjusted to give a range of pH by treatment with sulphuric acid or potassium hydroxide. The death of most of the worms under this highly unnatural treatment led Arrhenius, and influenced MOORE (1922), PHILLIPS (1923) and SALISBURY (1923) towards the view that earthworms flourish only in soils at, or about, the neutral point. OLSON (1928), in Ohio, however, found populations of *A. caliginosa* f. *trapezoides* (Duges) and *L. terrestris* in field soils of pH 5·45 while BORNEBUSCH (1930), working on Danish forest soils, found *A. caliginosa* plentiful in soil of pH 5·4–5·2. Where the pH of the upper soil was 4·3 or below Bornebusch found that earthworms were few and the surface living *Dendrobaena octaedra* (Sav.) predominated.

The distinction made by Bornebusch between acid-tolerant litter-dwelling species and acid-intolerant burrowing species is supported by the writer's observations in the Lake District where earthworms were collected from 36 woodland sites ranging in soil reaction from pH 3·7–8·8. There is, however, a third group which is more ubiquitous and diverse in habits. Data of the occurrence in these Lake District woods of representatives of these three groups are given below:

TABLE 22

Occurrence of acid-tolerant, ubiquitous and acid-intolerant species of earthworms in Lake District woodland soils

pH (*upper 10 cms*)	*Sites examined*	% *with* B. eiseni *acid-tolerant*	% *with* L. rubellus *ubiquitous*	% *with* Allolobophora *sp. acid-intolerant*
Below 4·5	22	82	45	0
Over 5·0	13	8	77	92

Thirteen of the commonest species of earthworms taken in the Lake District and Park Grass are classified below (*Figure 39*) according to the pH values of the soil or litter in which they were found. The three ' acid-tolerant ' species are all surface dwellers and the five ' acid-intolerant ' species all live in mineral soil, but in the ' ubiquitous ' group *Dendrobaena subrubicunda* (Eis.) and *Lubricus castaneus*

are mainly surface dwellers, *Octolasium cyaneum* and *Lumbricus terrestris* form deep burrows, and *Lumbricus rubellus* either lives in litter or burrows in mineral soil according to the situation.

Sites are occasionally found where 'acid-tolerant' and 'acid-intolerant' species occur together. In a Lake District wood, for example, *Bimastus eiseni* (Lev.) was aboundant in leaf litter of pH 4·2, while the mineral soil of pH 5·4 contained *Allolobophora chlorotica*, *A. caliginosa* and *Eisenia rosea*.

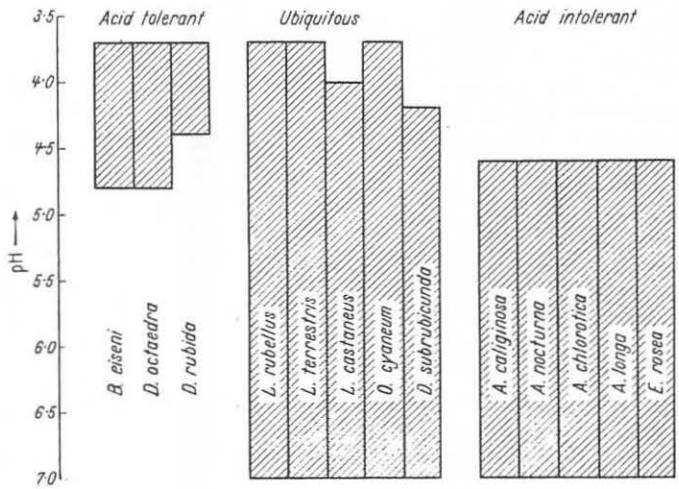

Figure 39—Classification of earthworm species according to pH *of litter or soil in which they were found.*

To summarize the investigation so far, pH has been shown to be a factor of prime importance in determining the limits of distribution of earthworm populations under natural and experimental field conditions.

RELATIONSHIP OF BIRTH AND DEATH RATES TO AGGREGATION IN EARTHWORM POPULATIONS

In the Park Grass analysis it was seen that about half the 'between plots' variance could be accounted for by the soil pH but, as may be seen from the high standard errors of the population means (Table 19), there are also some substantial population differences within plots requiring explanation.

The distribution of earthworms within plots was examined by calculating the 'index of dispersion' (FISHER, 1925 *et seq.*) which can be used as a χ^2 variate for detecting non-random distributions.

This index was calculated for the distribution of each species found in all the plots sampled and four significantly aggregated populations were found, two of *Eisenia rosea* and two of *Lumbricus castaneus*.

TABLE 23

Earthworm populations of Park Grass plots showing aggregated distributions

	Plot	*Species*	*Index of dispersion*
1951 (4 samples per plot)	8 L	*L. castaneus*	8·284
1952 (10 samples per plot)	7 L	*E. rosea*	26·890
1952 ,, ,, ,, ,,	9 L	*E. rosea*	17·811
1952 ,, ,, ,, ,,	13 U	*L. castaneus*	19·759

Value of χ^2 at 5 per cent significance level for 3 degrees of freedom (1951) = 7·815
Value of χ^2 at 5 per cent significance level for 9 degrees of freedom (1952) = 16·919

Guild (1952) recorded non-random variations in the earthworm populations of Scottish hill pastures and thought that local variations in soil moisture, acidity, organic matter and herbage cover were responsible for aggregations. On the Park Grass plots, which have been treated with great uniformity for almost a century and where the irregular manuring and grazing effects of stock are excluded, such variations appear to be too small to account for the large population differences. The data of Table 24 show that soil moisture and loss on ignition values of individual plots are very uniform, and in view of the lack of any detectable role which much greater differences in these factors played in accounting for the 'between plots' variance their variation within plots seems insignificant.

The data of Table 25 show that the plots are similarly uniform in soil reaction and, in any case, the pH values of two of the plots with aggregated earthworm populations are well above the level where acidity acts as a limiting factor.

TABLE 25

pH values of some Park Grass plots in May 1951

Plot	3 U	3 L	8 L	13 L	17 L
Sample 1	4·6	6·9	6·5	6·5	7·0
Sample 2	4·8	7·0	6·5	6·6	6·7
Sample 3	4·6	7·0	6·5	6·5	6·8
Sample 4	4·6	6·6	6·4	6·6	6·8

It is possible, and indeed almost certain, that these measurements of physical, chemical and biotic characteristics of the plots have

TABLE 24

Moisture content and loss on ignition of three plots with aggregated earthworm populations

Plot	*7 L*					*9 L*					*13 L*				
Sample	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
% *Soil moisture*	29·2	27·5	27·8	27·9	23·4	28·3	29·1	26·3	29·0	29·5	27·8	26·7	27·0	26·3	28·4
% *Loss on ignition*	10·4	9·5	9·6	9·3	9·7	12·4	11·8	11·9	11·6	12·4	9·2	8·7	8·6	8·6	9·0

failed to reveal some varying factor or combination of factors in the environment which is really important in the life of the earthworms and which if detected might account for their aggregated distribution. There is also, however, the possibility that these aggregations have little or nothing to do with such spatial variations in the environment but arise from changes in the relation of reproduction rates to dispersion rates. If a randomly distributed population reproduces more rapidly than the offspring can disperse, the effect will be to produce a series of ' family ' groups, some of the groups overlapping to form aggregations of various sizes. If aggregations are in fact related to population dynamics in this way, it might be expected that those species where populations fluctuate most would also show the greatest tendency to form aggregations. It seemed significant, therefore, that the two species, *E. rosea* and *L. castaneus*, in which aggregation on the Park Grass plots was detected, were also the ones which showed the greatest difference between the population means (Table 26) of March 1951 and March 1952.

TABLE 26

Comparison of populations 1951 and 1952. Mean numbers per square feet of 8 plots

	1951	*1952*	*Difference*
E. rosea	4·565	1·933	−2·632
L. castaneus	3·170	1·912	−1·258
O. cyaneum	1·413	0·844	−0·569
L. terrestris	1·860	1·619	−0·241
A. nocturna	0·643	0·497	−0·146
A. caliginosa	1·829	1·927	+0·098
L. rubellus	0	0·013	+0·013
A. chlorotica	0·086	0·085	−0·001

Furthermore, the distribution of adult earthworms and immature stages supports this interpretation of the aggregations. When the index of dispersion was calculated for the adults their distribution was found to be random while the aggregation was accounted for entirely by the young earthworms (Table 27).

This was the situation on Park Grass in April 1952. A month later, on an adjacent pasture field, the situation was the same with *E. rosea*, but with *L. castaneus* both adult and immature stages were aggregated. This species matures more rapidly than *E. rosea* and the adults in May would be mainly the newly matured generation, probably not yet dispersed from the ' family ' grouping. This interpretation is supported by the much higher proportion of mature to immature specimens in the May population (Table 28).

TABLE 27

Population distributions of mature and immature earthworms in April (1st week) 1952 (10 samples per plot)

	Plot	Adults as % of total	Index of dispersion		
			Mature	Immature	Total
E. rosea	7 L	38·1	6·118	27·921*	26·890*
E. rosea	9 L		7·225	17·811*	17·811*
L. castaneus	13 U	21·3	4·685	23·286*	19·759*

* Aggregated populations
Value of χ^2 at 5 per cent significance level = 16·919

In the populations of six of the species tested (Table 28) the value of the index of dispersion for the population as a whole is greater than that for the mature and immature stages considered separately. This shows that mature and immature individuals of the same species tend to occur in groups together and these might be interpreted either as concentrations in places where soil conditions are favourable or as indicating a stage in the maturation of the 'family' groups when dispersal is beginning to weaken the aggregation.

TABLE 28

Population distribution of mature and immature earthworms—May 5 1952

	Mean No. per square yard	Adults as % of total	Index of dispersion		
			Mature	Immature	Total
L. castaneus	3·6	57·0	107·78*	116·51*	204·28*
A. chlorotica	1·5	61·3	87·84*	45·33	152·68*
E. rosea	3·2	49·8	80·31	124·92*	106·20*
A. nocturna	20·6	38·2	81·66	93·01*	98·55*
A. caliginosa	10·8	20·3	52·00	77·10	85·43*
L. terrestris	9·2	11·7	65·49	77·36	87·86*
O. cyaneum	1·3	23·8	69·60	64·00	71·43
Total (3217)	50·3				162·75*
Total excluding *L. castaneus*	47·5				130·61*

* Aggregated populations
Value of χ^2 at 5 per cent significance level = 82·50

From the examination of Park Grass as a whole it was seen that although individual species differ in their ecological requirements, nevertheless most of the species were abundant together on the

favourable plots and scarce on the unfavourable plots. It might therefore be expected that if the earthworm aggregations represent concentrations in places where soil conditions are favourable, or food abundant, the aggregations of different species would tend to occur together in these places. However, the index of dispersion of the total population is considerably less than that of *L. castaneus*, and when this species is excluded the value of the index for the remainder is less than that for *A. chlorotica*. This shows that although the adult and immature stages of the same species tend to form aggregations together, the aggregations of the different species tended not to occur in the same places and this perhaps supports the view that the aggregations are related to ' family ' groupings rather than to environmental conditions.

3	2	9	4	2	3	14	6
2	1	1	9	4	5	7	2
2	0	3	9	12	0	4	0
4	0	3	8	14	2	6	2
7	0	0	0	6	7	4	6
7	1	7	2	1	2	4	3
3	1	0	0	1	0	2	1
3	5	5	0	5	1	1	0

Double hatched - more than 8 L. castaneus per square yard
Single hatched - 5-8 L. castaneus per square yard
Unhatched - less than 5 L. castaneus per square yard

Figure 40—Distribution of L. castaneus *in a quadrat 8 × 8 yards.*

In *Figure 40* an area in this site is shown where the density of *L. castaneus* is particularly high over several square yards. It might be objected that an aggregation of this size is too large to be accounted for on a ' family ' basis. It does not, however, necessarily

represent a single season's progeny from one or a few worms, although, with the annual reproductive rate of 65 cocoons per individual, given for this species by Evans and Guild (1948), this appears not improbable. Large aggregations of species with low reproductive rates such as *E. rosea*, for which Evans and Guild gave the figure of eight cocoons per annum, would seem more likely to be the product of several seasons in which conditions have continued to favour the aggregating effect of reproduction more than the randomizing effects of mortality and dispersion. Under such circumstances neighbouring aggregates might expand until they merged, giving again a random distribution: the detection of aggregation would then become a problem of selecting an appropriate sample size.

To conclude, several species of earthworms, particularly the very active surface-living *L. castaneus*, are commonly found concentrated around old dung-pats or similar food sources. Aggregations also occur, however, in situations where the habitat seems to be very uniform and although this may be a reflection of our ignorance of what factors really affect earthworm distribution, nevertheless much of the irregularity of distribution may be related more to changes in the populations' vital coefficients than to spatial variations in the environment.

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DISCUSSION

MR. J. A. SVENDSEN (Zoology Department, University of Durham): Certain species of earthworm are surface living and constantly active, at least when the soil surface is wet. Aggregations occur when these species stay a little longer than usual in any given spot because it is a particularly suitable environment, for example, in dung.

I should like to make a plea for the replacement of the term ' earthworm ' by the family name Lumbricidae. Other English-speaking countries use 'earthworm ' for any large terrestrial Oligochaet, for example, the 'oriental earthworm ' *Pheretima.* Similarly, general descriptions of the behaviour or habitats of earthworms should be avoided. The biological information available shows such wide differences between the habits of the species that the use of the collective term makes the information meaningless. It also follows that work which fails to distinguish between species of Lumbricidae is now quite useless.

To turn to sampling methods; Lumbricid workers have no entirely suitable quantitative method. Both my own work (see page 364) and that of Dr. Satchell have shown the standard permanganate technique to be unreliable. Similarly the electrical method of Dr. Satchell fails to extract

more than a proportion of the total population. I find it difficult to assess the value of results which entail the application of statistical treatments to population estimates of unknown accuracy.

Dr. W. J. McL. Guild: I agree with Mr. Svendsen that many species of earthworms move over the soil surface under wet surface conditions. This may be one method of species spread to new areas.

On sampling I would say we all appreciate the difficulties of sampling, but existing methods have their advantages. The electrical method designed by Dr. Satchell may be quite a good qualitative method under certain conditions. The permanganate method also has advantages under some conditions, but on balance its disadvantages outweigh its advantages. At present the most reliable sampling method still remains digging and hand examination.

Mr. G. W. Heath (Grassland Research Institute, Hurley): I was interested to note that Dr. Guild specifically mentioned earthworms feeding on cow and horse dung (see page 90) and did not mention sheep dung; I would like to know if there is any evidence concerning this point. I have not myself found any difference in earthworm populations (measured by weight) on plots grazed by sheep as opposed to a 'cut and carry off' treatment with no animals on the plot. This is not in agreement with the findings of workers in New Zealand nor those at Wye, Kent, who have obtained increased earthworm populations on plots where dung and urine are retained. These workers have, I believe, only been sampling to a depth of 2–3 inches and I think this may have led to a false estimate of the total population.

I have in my own experiments found a significant increase in the weight of earthworms on plots under a three-year ley as opposed to a normal arable four-course rotation. I have also obtained some correlation between weight of earthworms and the increase in water stable aggregates on these plots. With regard to Dr. Satchell's concept of the 'family group' as an explanation of aggregation in field populations, I think this a very valuable contribution to a difficult problem. In addition it might be, however, that the apparent aggregation of populations is a reflection of our inability to sample the population in a satisfactory manner.

Mr. O. Gilbert (Nature Conservancy, Grange-over-Sands): With regard to Dr. Satchell's laboratory experiments I wish to ask two questions: (1) In one experiment concentration of sulphate was varying with hydrogen ion concentration. What is the effect of varying sulphate while holding pH constant ? (2) Did Dr. Satchell attempt experiments varying pH in the presence of calcium ions ? I believe that calcium may have an important effect on soil animals quite apart from nutritional considerations. As Mr. Blower suggested in his paper calcium ions in the soil water may exert a profound effect on the water relations of soil animals.

Dr. Satchell: In answer to the first question, only the variation of pH was investigated in that experiment since the field data did not suggest an important effect of sulphate ions on earthworm distribution. On the second point pH was varied in the presence of calcium ions in the experi-

ment with *Allolobophora chlorotica* but the violent reaction of the earthworms was too rapid to be explained as an osmotic effect.

MR. J. G. BLOWER: Substantiating Mr. Gilbert's remarks, I, too, consider the possibility of endosmotic uptake of water by earthworms to be an important point. Two pieces of evidence from Dr. Satchell's paper point to this. First, the confinement to the surface of acid-intolerant species would suggest that the lower soil layers may be inimical to these animals because of their inability to limit water uptake (by calcium ions). Secondly, the observations of Drs. Guild and Satchell and of Mr. Svendsen, that worms are more active in damp surface layers, would suggest again that dampness was inimical to the animals. Another point may be raised: does Dr. Satchell know of any attempt to relate the iso-electric point of the surface mucous to the usual pH obtaining in the habitat, since the viscosity *etc* of mucous must be important to the animal.

DR. SATCHELL: On the iso-electric point no information is available. Regarding the water uptake and calcium ion concentration, certain species will survive for a long time under water. I have kept *Octolasium cyaneum, Allolobophora caliginosa* immersed in water for six weeks at a time without their showing any ill effects.

MR. BLOWER: Yes, but an earthworm in water will be—by analogy with other groups—doing three times the amount of work that is necessary; a large part of the metabolic activity will be necessary, merely to bail out water which enters the worm and thus there will be a great advantage to be gained from living in a situation where this 'wasted' work is not necessary.

MR. SVENDSEN : I wish to make it clear that I did not imply that Lumbricids travel in damp surface soil but that certain surface-living species are constantly active on the surface so long as conditions are suitably wet. In respect of their water relations these species are particularly active under very wet conditions which suggests that they have some mechanism by which they avoid water absorption.

PROFESSOR W. L. KUBIENA (from the Chair): I should like to draw attention to the presence of earthworms in arid soils. The presence of earthworms distinguishes a semi-desert from a desert soil. It would be most valuable to find a good way to extract earthworms from arid soils in which they may lie deeply buried.